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to the same organ by different diseases, or to different organs by different diseases—have been worked out. Only 4 of these—that is only about one case out of six—are exceptions to the rule that varieties which show more than the average amount of injury by one disease will, on the whole, show more than the average injury by another disease. No one of these exceptional constants can be considered significant with regard to its probable error. Several of the 19 which indicate the rule may be looked upon as individually trustworthy. Thus notwithstanding the large variations in numerical magnitude incident to small series of data and rough measurement, the determinations taken collectively certainly furnish highly convincing evidence that to a considerable extent susceptibility to disease is general rather than specific.

The fact that the series of correlation coefficients here presented justify much more definite conclusions than those who have considered the data without statistical analysis have drawn, is sufficient indication of the usefulness of the biometric method in the preliminary stage of disease-resistance experiments in which large numbers of strains are being tested, and in which the mass of data is highly confusing. The special cases illustrated by no means exhaust the possibilities of the biometric formulæ now available. Had the data been more extensive, the analysis might have been carried much farther.

Nothing that has been said in this paper in emphasis of the statistical method must be taken to imply that the most careful individual analysis is not desirable and essential. The two methods are not mutually exclusive, but supplemental.

J. ARTHUR HARRIS

THE DIFFERENT MEANINGS OF THE TERM "FACTOR" AS AFFECTING CLEARNESS IN GENETIC DISCUSSION[1]

IN the analysis of alternative (or segregating) heredity, we find that certain potentialities, such as that of producing a certain color in some part of the soma, appear to be inherited independently of certain other potentialities. We assume that the germ-plasm carries various corresponding genes, factors, or determiners, whose independence in gametogenesis determines the independence of the somatic characters. Cytological study leads to some very probable conclusions as to the time and method of segregation of these determiners; though it does not yet enable us to identify with absolute certainty the actual physical unit of segregation, the cytological and genetic evidence indicates strongly that such a unit exists.

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[1] Paper No. 39, University of California, Citrus Experiment Station, Riverside, California.

In the current chromosome hypothesis, as developed especially by Morgan and his collaborators (Morgan, Sturtevant, Muller, and Bridges, 1915), the material unit of segregation is assumed to be a part of a chromosome. Breaks in two homologous chromosomes at meiosis, with consequent exchange of parts by the pair, presumably occur at certain definite points only. How close these points may be we can not say, but the general stability of Mendelian characters indicates that the number of points is limited. On these assumptions, the portion of a chromosome between two adjacent points of possible breaking is the ultimate physical unit of genetic segregation—essentially a *locus* as defined by Morgan (1915, p. 419).[2]

It is now widely recognized that, in effect, a single real unit of segregation may influence very diverse characters of the soma, often in ways which can not be at all inferred one from another. Very possibly one physical unit of segregation may affect, say, flower color and height in ways just as distinct physiologically as may two distinct units of segregation, although transmission is different in the two cases. In the latter case we say that two genetic factors are concerned; are we compelled in the former case to admit only one?

As a matter of fact, as will be evident on further consideration, either course is possible, according to the definition of *factor* accepted.

If by "factor" we mean a *developmental potentiality*, the delimitation of a particular factor is largely a matter of convenience in analysis. On the other hand, if the term is used to designate a supposed actual physical unit of segregation, a factor has a definite objective extent.

The former view is that of the presence-and-absence terminology, as it is generally understood at present. In this sense, a factor is not an element of the germ-plasm; it is rather a property or characteristic of the germ-plasm or of some element of the germ-plasm. The characters of an organism, as Gates (1914,

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[2] Though Morgan, Sturtevant, Muller and Bridges (1915, p. 155) suggest the possibility that the loci of linked factors may be so near together in a chromosome "that they never (or very rarely) cross over." The definition of *locus* is discussed below.

p. 269) has remarked, are "attributes," no more to be separated from the organism than are the properties of a chemical compound from that compound. The factors of the presence-and-absence scheme, similarly, are inferred *properties or attributes of the germ-plasm,* by whose behavior we explain the alternative transmission of certain properties or attributes of the soma.

Obviously an organism is not composed of "characters"—and neither is its germ-plasm composed of "factors," so long as the factors are those of the presence-and-absence scheme. Such factors are nothing but *characters of the germ-plasm,* and, like the characters of the soma, they are more or less conventionalized in description. We have no warrant for projecting these conventionalized descriptions back into the actual germ-plasm, and assuming the presence and absence there of strictly corresponding material units of segregation.

The presence-and-absence scheme, when not encumbered with non-essential hypotheses, is a strictly neutral instrument of genetic analysis. If there is segregation in the formation of the germ-cells, it is merely a matter of definition to state that a factor is allelomorphic to its absence. That is, the assumption of segregation is the only assumption required by this scheme, which is the logically simplest form of the "conceptual notation" (East, 1912) of genetics.

Very special emphasis must be placed on the fact that the "absence" is absence of a *potentiality,* without reference to the presence or localization in the germ-plasm of any other potentiality that may actually take its place. The allelomorphism of the presence-and-absence notation is a *logical* opposition; when it makes "A" and "no-A" allelomorphs, this involves no assumption as to what may be physically opposed, in the chromosomes, to the physical basis of "A."

If an "absence" a of a given factor A is always or commonly accompanied by an actual presence of a corresponding factor A', and we wish to represent this fact, it is provided for by the terminology of linkage; we may use $\overset{\frown}{Aa'}$ and $\overset{\frown}{aA'}$, since the presence-and-absence scheme makes no assumptions as to the structure of the germ-plasm. It is obviously simpler to write simply A and A', or A and a, for the two factors, and convenience may justify this practise; we should note, however, that in thus abandoning the presence-and-absence terminology we introduce a second assumption, that of actual factor-to-factor opposition or allelomorphism. This assumption is, of course, in view of all the evidence, a highly probable one, and especially convenient in cases of apparent multiple allelomorphism (Morgan, Muller, Sturtevant, and Bridges, 1915, chap. 7). In fact, this added assumption probably permits a more direct and therefore practically simpler representation of the actual course of segregation. Whether the corresponding factor-to-factor notations now used for Drosophila (Castle, 1913; Morgan, Sturtevant, Muller, and Bridges, 1915, p. 233) are everywhere adequate and convenient is another question, as Emerson (1913) has shown.

Cases of multiple allelomorphism involve no special difficulty *in principle* for the presence-and-absence scheme. They can of course be represented only by linkage formulæ, in which the "presence" of one factor of the set is linked with the absence of the rest—but their very occurrence suggests that we might, as is suggested above, correctly enough represent single factorial differences in the same way. All this can affect only the convenience of the notation, and not at all its logical applicability.

If we adopt a factor-to-factor system of notation, it is natural to conceive of the opposed "factors" not as mere potentialities, but as physical units responsible for genetic potentialities. When we have taken this viewpoint, we have begun to use the word *factor* in the second sense mentioned above; we are thinking of assumed physical units of segregation, not merely of observed potentialities of development. Morgan (1915, p. 419), in discussing "presence and absence," uses *factor* in this sense, as do Morgan, Sturtevant, Muller, and Bridges (1915, pp. 220–222).

No doubt what has been said above is an old story to experienced geneticists in general, in view of such discussions as those of East (1912) and Morgan (1915). The distinction is so fundamental, however, and the double use of the term *factor* so increases the difficulties of the case, that consideration of the general problem from the present terminological viewpoint seems highly desirable. Perhaps greater precision in the use of several terms could be attained.

Johannsen (1909, pp. 124–125), in defining the term *Gen* (gene), makes it perfectly plain that he means the material basis[3] or cause (the *Anlage*), of whatever sort, of a "unit character," defining a *unit character* as one dependent on a special kind of gene. He is evidently inclined to consider the gene as the material unit of segregation, holding that the sum of the genes constitutes the germ-plasm, and there is a widely prevalent tendency among geneticists to use *gene*, and its synonyms *factor* and *determiner*, in this sense, which is the second of the two discussed above. Evidently *gene* is not properly used in the first sense. A moment's thought, however, will show the impracticability of confining *factor* to that sense; the meaning of this term shifts back and forth continually in common usage, and often remains indefinite.

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[3] Or *immaterial* basis, if we must admit the theoretical possibility of the existence of immaterial "entelechies" associated in some more or less mystical way with the germ-plasm.

Further, when *factor* (or *gene*) is used in the second sense, we consider it coextensive with *locus* (Morgan, 1915, pp. 419–20; Goodspeed and Clausen, 1917, p. 32). A factor is a particular state or condition of a locus. Let us, then, define *locus* as the physical unit of segregation, almost certainly identified as a genetically indivisible portion of a chromosome. Genetically inseparable (''completely linked'') potentialities, then, belong to the same locus, and hence to the same factor or gene; ''completely linked factors'' are mainly[4] relegated to non-cytological discussion, and especially to use with the presence-and-absence terminology.

No doubt Mendelian analysis considers, in any case, only some of the most readily identifiable properties of the real units of segregation concerned, and this fact seems to deserve a large place in our genetic thinking. Especially is it important that the two meanings of *factor* and its synonyms should be clearly distinguished; when these meanings are unconsciously interchanged and confused, vagueness and misunderstanding are sure to result.

The student of genetics may read, for example (East, 1912),

> If we forget ourselves and begin to speak of unit factors as particles, only a confusion follows similar to that caused by Nägeli, Spencer, and Weismann. Nothing is gained and even facts are obscured.

On the other hand, he will find the factors of *Drosophila* located with mathematical exactness in diagrams of the chromosomes, and often apparently or explicitly considered as material components of the chromosomes. In the interest of clear thinking, especially in the case of beginners and casual students in the field of genetics, the explanation of this apparent contradiction deserves very special emphasis.

As an example of the way in which this terminological conflict may cloud an argument when the essential facts are clear to the writer, we may take the following case. Morgan (1913,

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[4] Obviously, temporarily complete linkage of genes must be excepted, as in the usual case with the male of *Drosophila*. The point is that the chromosome theory may well consider, in any case, that potentialities *always* associated are manifestations of the same factor or gene.

p. 10), in urging his substitute for the presence-and-absence scheme, largely on grounds of convenience, agrees with East (1912) as to the general usability of the latter scheme as a "system of nomenclature" without cytological implications. He makes especially plain the undesirability of interpreting "absence" as a physical absence in the germ-cell, or (1915, p. 419) as "a hole in a chromosome." In one respect, however, Morgan's discussion seems less clear than it might be, and this is in the use of *factor*, in these articles, in a sense (the second here) which is not that of the presence-and-absence scheme, with only vaguely implied explanation of the distinction. It certainly *is* permissible to speak of "the absence of a factor from the germ-plasm," *if we mean the kind of "factor" implied by the presence-and-absence terminology.*

We must make it as clear as possible that *factor* (1) sometimes means a potentiality and (2) sometimes means a body, and that a factor is assumed to be paired either (3) with its absence or (4) with another (identical or different) factor. The combination of (1) and (3), then, gives the presence-and-absence scheme, while the combination of either (1) or (2) with (4) gives the scheme used by Morgan (1913; see also Castle, 1913) and other students of *Drosophila.* General objections to Mendelian analysis have been based largely on confusion of (1) and (2), which often leads to erroneous suppositions—for instance, that Mendelian analysis in general, or the presence-and-absence method of Mendelian analysis, requires the unnecessary and unwarranted assumption involved in the combination of (2) and (3). Probably this confusion is also largely responsible for the persistence of another often discredited notion, the idea that "Mendelians" suppose their factors to be individually the basis of somatic characters, rather than simply necessary elements in an interacting complex which produces the characters.

SUMMARY

The term *factor* has, in genetic use, two distinct meanings, which are continually interchanged or combined and often confused. It is essential to clearness in genetic discussion that these two meanings should be carefully distinguished. These meanings may be indicated by the following formal definitions:

1. A genetic (Mendelian) factor is a property or characteristic of the germ-plasm, more or less conveniently delimited for the purpose of analysis of segregating heredity.
2. A genetic (Mendelian) factor, or gene, is an actual material

unit of genetic segregation; it is of unknown nature, but probably consists of a genetically indivisible portion of a chromosome (a *locus*) in a particular state.

The presence-and-absence scheme of factor notation properly employs only the first of these meanings; the Morgan-Castle scheme, on the other hand, may use either.

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THE SELECTION PROBLEM

Unless history fails to repeat itself, geneticists, whose attention is focused upon variation, should sooner or later overemphasize its importance as a factor in shaping the organic complex. There is, indeed, reason to believe that already a tendency for some among them to do so is becoming apparent. Dr. Pearl's[1] recent paper under the title above affords an example in point.

In that communication its author fails to discriminate sharply between two distinct phases of his subject. Whether selection may affect the course of evolution is a matter entirely apart from the possibility that it alters the germ plasm. Racial history may possibly be modified, if the genetic composition of a mixed population may be affected by selection based upon somatic dif-

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[1] Pearl, Raymond, 1917, "The Selection Problem," The American Naturalist, Vol 51, pp. 65–91.